

A review of amphidromous freshwater fishes of the Chocó biogeographical region (Colombia and Ecuador): diversity, ecology, fisheries and conservation

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Abstract. – Amphidromy is a specialized form of diadromy developed by tropical and temperate fish and invertebrates. In the tropics, most amphidromous fish belong to the Gobiidae and Eleotridae families. Knowledge on the taxonomy, phylogenetics, ecology, fisheries and conservation of this group of fishes has been gathered in the last 30 years mainly in the Indo-Pacific and Caribbean regions, with the tropical Eastern Pacific region largely overlooked in literature. Here, we provide a state of the art review on the ecology, fisheries and conservation of amphidromous fishes in two countries of the Chocó biogeographical region (Colombia and Ecuador). We then focus on different observations carried during the last 10 years at three main localities (El Valle – Chocó, Delta del Rio San Juan and Dagua Basin) with contrasting environmental settings in the Colombian Pacific coast where amphidromous fishes are harvested by Afro-Colombians and Indigenous people. Accelerated environmental changes (*e.g.* mining, deforestation, water pollution) in the catchment areas of the rivers draining into the Pacific Ocean may threaten the populations of several of these amphidromous fishes. Understanding further ecological aspects of amphidromous fishes in this region will greatly benefit further global comparisons.

Résumé. – Revue des poissons d'eau douce amphidromes de la région biogéographique du Choco (Colombie, Équateur): diversité, écologie, pêche et conservation.

L'amphidromie est une forme spécialisée de diadromie développée par les poissons et les invertébrés des zones tempérées et tropicales. Sous les tropiques, la plupart des poissons amphidromes appartiennent aux familles des Gobiidae et des Eleotridae. Les connaissances sur la taxonomie, la phylogénie, l'écologie, la pêche et la conservation de ce groupe de poissons se sont concentrées ces 30 dernières années principalement dans l'Indo-Pacifique et la région Caraïbe, mais la région du Pacifique tropical oriental a été en grande partie négligée dans la littérature. Ici, nous fournissons un état des connaissances de l'écologie, de la pêche et de la conservation de ces poissons dans deux pays de la région biogéographique du Choco (la Colombie et l'Équateur). Cette étude provient des différentes observations réalisées pendant les 10 dernières années, principalement au niveau de trois sites (El Valle – Chocó, delta de la rivière San Juan et bassin de la rivière Dagua) de la côte colombienne Pacifique où les poissons amphidromes sont consommés par les communautés indigènes. Les changements environnementaux (exploitation minière, déforestation, pollution de l'eau) qui s'accélèrent dans les rivières menacent les populations de ces espèces. Comprendre l'écologie et le cycle de vie de ces derniers dans cette région est le principal challenge afin d'assurer leur gestion et conservation.

Key words
Gobiiformes
Mugiliformes
Chocó Biogeographic Region
Amphidromy
Artisanal fishery
Conservation

The Chocó Biogeographic Region (CBR) extends from the Panamanian province of Darién in Colombia to the province of Manabí in southern Ecuador, between the Pacific Ocean and the watershed of the western slope of the Andes mountain range (Díaz-Merlano and Gast-Harders, 2009). This region is characterized by heavy rainfall that gives rise to a large number of rivers and streams running through a complex river network that shelters an ichthyofauna that, although it is not the most diverse, is of high value because of the level of endemism (Abell *et al.*, 2008; Maldonado-Ocampo *et al.*, 2012; Jiménez-Prado *et al.*, 2015). However, within the species that inhabit the aquatic ecosystems of the region, there are amphidromous species, which despite their economic, ecological and cultural importance, have been poorly studied, presenting information gaps on the taxonomy of some species, their biology and even the interactions

they have with the environment and other species.

According to McDowall (2010) and Keith *et al.* (2015), amphidromy is characterized mainly by the fact that spawning, egg development and hatching occurs in fresh water, then the larvae are swept to the ocean. Here they dispersed during one to several months depending on the species (Iida *et al.*, 2009; Lord *et al.*, 2012; Taillebois *et al.*, 2012), and later as post-larvae they return to fresh water and complete their growth in rivers and streams, where they obtain food, live permanently and mature for later reproduction (McDowall, 2010; Watanabe *et al.*, 2014; Blanco-Libreros *et al.*, 2015). For this, they require special conditions such as steep topography with short rivers that assist the dispersal of the larvae towards the ocean, which is why this is a diverse group in the Caribbean or the Indo-Pacific islands.

Amphidromous species are poorly represented in con-

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tinental zones (Ebner *et al.*, 2011), with few species recognized in South America, especially Sicydiinae gobies (McDowall, 2010). On the other hand, ravines and insular rivers in the CBR remain poorly explored, with few inventories and little integral knowledge of the functioning of communities and ecosystems (Blanco *et al.*, 2014).

The accelerated increase in productive activities in the region generates deforestation, contamination by wastewater discharge and modification of channels, which all have a direct influence on continental and coastal aquatic ecosystems. This situation endangers the populations of amphidromous species that require connectivity between the rivers and the sea to complete their life cycle involving migrations (Walter *et al.*, 2012; Keith *et al.*, 2015); it may increases the decline or loss of species that have not even been discovered or studied in a region characterized by a high level of endemism.

The present work offers an overview of the current state of knowledge on valid amphidromous fish species that have been recorded in the Pacific Region of the CBR (Colombia and Ecuador), summarizing aspects of their ecology, distribution and use by local communities and discussing the main factors that may jeopardize their persistence and conservation.

MATERIALS AND METHODS

Study site

The information comes from localities in the Pacific region of the CBR (Fig. 1), characterized by a great hydric wealth that in Colombia is mainly due to the presence in its eastern end of the western Andean mountain range and of the Baudó and Pacific highlands. These mountains serve as hydrographic centres, where in addition to giving birth to rivers, they form a natural barrier to the oceanic winds, which causes permanent rains and increased flow rates in rivers (Gutiérrez *et al.*, 2011). Here, the coastal or marine plains can be distinguished as landscape units, highlighting the fronts of the river deltas, with the coastal bars and cords and beaches and canals bordered by mangroves that are typical of the central-southern part of Colombia and northern Ecuador. It is also possible to distinguish hills and highlands separated from the mountain range with altitudes up to 500 m high that predominate in the northern Colombian Pacific including the Gorgona Island located to the south (Díaz-Merlano and Gast-Harders, 2009).

In Colombia, main records come from the Baudó, Buenaventura, Naya and Tumaco subregions (Fig. 2), while Ecuador information was taken from the coast subregion, in the hydrographical region of the Santiago-Esmeraldas river basins and the rivers that drain into the sea from the western slope of the western cordillera to the north of the country (Fig. 3).

From a freshwater fish bioregion perspective, the information relates to the region called “northern Andes Pacific watershed and Atrato River basin”, but with emphasis in the Pacific zone, characterized by highly endemic ichthyofauna, but with low species richness compared to other regions (Abell *et al.*, 2008).

Fish data source

Information on amphidromous fish species from the CBR on the Pacific watershed was obtained from a literature review, databases of fish collections registered in the Ecu-



Figure 1. – Map of the Chocó Biogeographical Region in the Pacific of Colombia and Ecuador.

dorian Museum of Natural Sciences in Quito and Museum of Natural Sciences Federico Carlos Lehmann Valencia-IMCN in Cali and unpublished data from the author. Synonymy and valid names were verified online with the California Academy of Sciences Catalog of fishes (Eschmeyer *et al.*, 2016) and current classification of fish groups was carried out according to Nelson *et al.* (2016).

Data on ecological aspects, species use and pressures over basins or species were obtained from different projects, expeditions and specific collections in which the author has participated in the last 10 years in different basins of the Colombian Pacific region, among which the Valle River in the North Pacific – Baudó subregion (2010), Dagua (2006, 2010, 2011, 2013, 2014, 2016), Anchicayá (2013, 2014, 2016), Calima (2013 and 2016) – and San Juan rivers (2015 and 2016) in the Buenaventura subregion and Río Cajambre (2008) and Yurumanguí (2012) in the Naya subregion at the central Pacific region of Colombia.

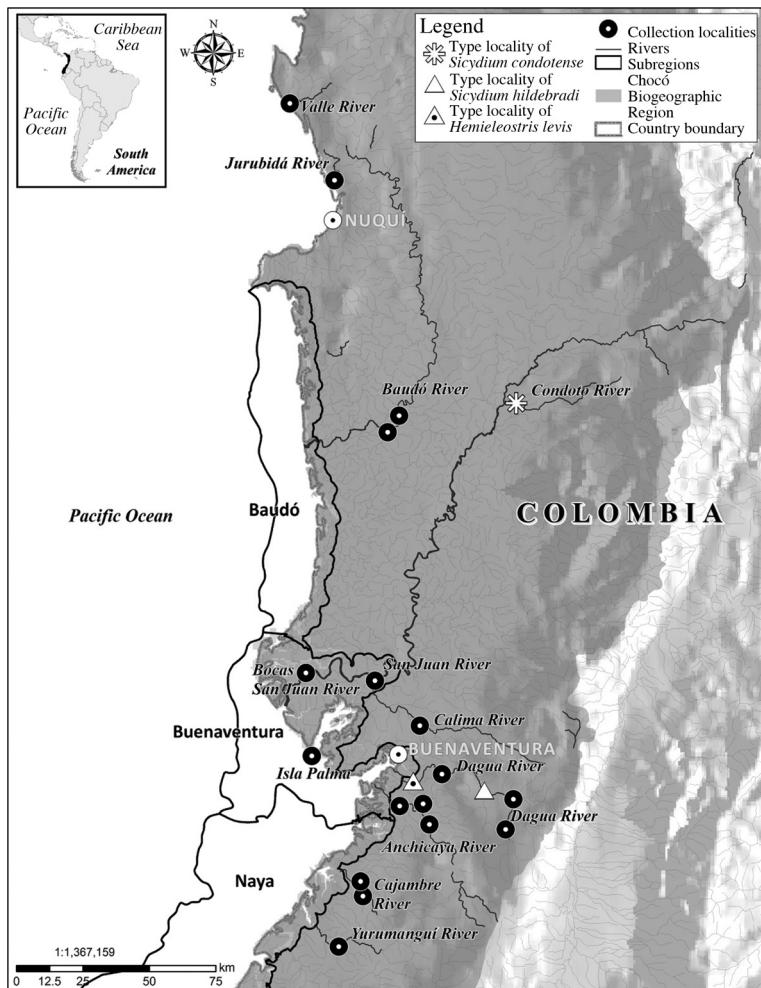


Figure 2. – Records of freshwater amphidromous fishes in the Pacific coast of Colombia.

RESULTS AND DISCUSSION

Species richness

For the Pacific Region at the CBR, 10 species considered as amphidromous were identified during migration in the post larval stage or in adult stage. The species are grouped into two orders (Gobiiformes, Mugiliformes), three families and seven genera. The family Eleotridae had the greatest species richness among the amphidromous with five species: *Dormitator latifrons* (Richardson, 1844), *Eleotris picta* Kner, 1863, *Gobiomorus maculatus* (Günther, 1859), *Hemileotris latifasciata* (Meek & Hildebrand, 1912) and *Hemileotris levis* Eigenmann, 1918. The Oxudercidae family (gobies) stands out with four species: *Awaous transandeanus* (Günther, 1861), *Sicydium hildebrandi* Eigenmann, 1918, *Sicydium rosenbergii* (Boulenger, 1899) and *Sicydium salvini* Ogilvie-Grant, 1884 (Fig. 4). Finally the Mugilidae family (mullets) was represented by one species: *Agonostomus monticola* (Bancroft, 1834), for which it is currently discussed whether it should be considered amphidromous or catadromous (McMahan *et al.*, 2012).

Distribution and ecology of amphidromous fishes of the Chocó Biogeographic Region

Most of the species recorded as amphidromous in the Pacific Region of the CBR have a wide distribution. *Dormitator latifrons*, *E. picta*, *G. maculatus*, and *A. transandeanus* have been reported from southern California and Mexico to Peru. *Hemileotris latifasciata* has been reported from Mexico to the province of Guayas in Ecuador (Nordlie, 2012; Jiménez-Prado *et al.*, 2015), while *H. levis* is endemic to the lower parts of the Baudó, Dagua and San Juan rivers in the central Colombian Pacific Region (Castillo and Rubio, 1987; Kullander, 2003). The Sicydiinae (*Sicydium* sp.) present a variable distribution, with *S. hildebrandi* presenting a northern distribution limit at the San Juan River basin and a southern limit at the Cayapas-Esmeraldas basin in Ecuador. *Sicydium rosenbergii* is endemic to the Santiago-Cayapas and Esmeraldas basins and *S. salvini* is distributed from México in Central America to the northern Pacific of Colombia (Lyons, 2005; Castellanos-Galindo *et al.*, 2011; Chabarría and Pezold, 2013). *Agonostomus monticola* has a wide distribution with occurrences in North, Central and South America along the Atlantic and Pacific oceans (McMahan *et al.*, 2012).

Larvae of *D. latifrons* have been reported throughout the Colombian Pacific coast with distances varying between 1–40 nautical miles

from the coast, salinities between 20.0-33.6 and temperature between 24.4-29.0°C (Beltrán-León and Ríos-Herrera, 2000). In Ecuador, larvae have been caught in the ocean and in freshwater streams (Jiménez-Prado *et al.*, 2015). Adults occupy different environments with presence in fresh, brackish and near shore marine water (Nordlie, 2012). In Bahía Málaga habitat preference was associated with soft substrates (Castellanos-Galindo *et al.*, 2006). In the Cajambre, San Juan and Yurumanguí river basins, adults and juveniles were found on the riverbanks, in streams, creeks and small temporary pools generated by floods in areas with muddy substrates with plenty of decaying plant material. Its distribution in freshwater is restricted to the lower parts of rivers and streams, reaching approximately 30m. (Sánchez-Garcés, unpubl. data). Some populations appear to exhibit a marginally catadromous or semi-catadromous life cycle, which consist of spawning, larval and post-larval development and sexual maturity in brackish water (Elliot *et al.*, 2007; Nordlie, 2012) however, most available information allows to determine that it is in fact an amphidromous species (Nordlie, 2012).

Post-larvae of *E. picta*, in the northern Pacific Region, in the Valle River have been observed in estuaries and ravines at the intertidal zone. In the central Pacific Region, in the islands of Bahía Málaga, they were associated with soft and hard bottoms (Castellanos-Galindo *et al.*, 2006), adults have been registered in rivers and ravines from 0-100 m high in hydro-morphological units such as pools and glides, with plant material and stone deposits and a preference for places with little current where they stalk their prey, being considered as a predator for fish and crustaceans. In Costa Rica's Pacific Region, Bussing (1998) reported that this species reproduces in freshwater, but spawning sometimes occurs in estuaries and river mouths, and it is possible that this behaviour also occurs in the coastal zone of Colombia and Ecuador. According to Nordlie (2012), some populations are likely to have an amphidromous life cycle, while others may have a freshwater or semi-catadromous migration pattern. Nevertheless, *Eleotris* species are generally amphidromous as stated by Mennesson *et al.* (2015).

In Colombia *G. maculatus* has been registered up to 100 m high and in Ecuador, catches up to 500 m high have been reported (Jiménez-Prado *et al.*, 2015). Post-larvae are common in the lower parts of the rivers in intertidal zones, while adults have a preference for rivers and streams in hydro-morphological units like pools and glides where the current is moderate to slow and the substrates are soft or hard, but with rocks and logs that serve

as shelter. In the Anchicayá river basin in Colombia, Ospina and Restrepo (1989) reported that this species has predatory habits, with shrimp and fish as main part of the diet. They have also observed that the gonads remained mature during the whole year, suggesting that this species does not have specific reproduction seasons. This concurs with what happens on the Ecuador coast, where spawning is prolonged, but displays intensity peaks during the months of January and July (Jiménez-Prado *et al.*, 2015). Despite being proposed as an amphidromous species, Nordlie (2012) considers that *G. maculatus* probably has a marginally semi-catadromous life cycle.

Hemileotris latifasciata, in adult stage, are often found in rivers and streams between 0-120 m high. It is an abundant species that prefers the shallow banks of hydro-morphological units like pools and glides with sandy substrates and gravel containing deposits of vegetal material. The little information that existed until a few years ago did not allow determining whether it was an amphidromous or marginally

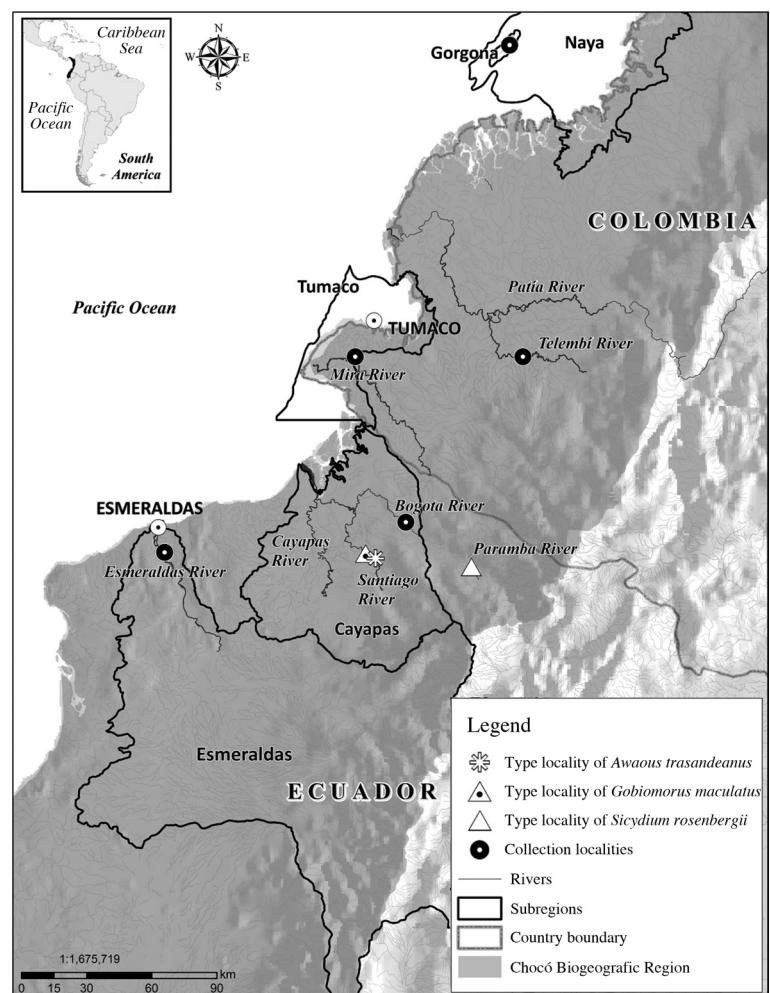


Figure 3. – Records of freshwater amphidromous fishes in the Pacific coast of Ecuador.

cataudromous species or even a purely freshwater species (Nordlie, 2012). However, post-larval migrations from the ocean to the rivers were recently evidenced indicating that *H. latifasciata* has an amphidromous life cycle (Sánchez-Garcés, unpubl. data).

As for *H. levis*, little information is available on this species. There are only seven occurrences in databases, corresponding to (i) the type specimens from which the species was described in 1918, coming from pools near the Dagua River, and (ii) to samples obtained in the years 1945 and 1989 in the Baudó River basin. These specimens are deposited in the Museum of the California Academy of Sciences with records corresponding to sites between 0-12 m high. There is little information on the ecology of this species, but field notes of the type material refer to catches in pools with very high water temperature (Eigenmann, 1922). Recent observations of post-larvae kept in captivity, have allowed recognizing that it is a species with a preference for environments without current and very tolerant to remain outside the water. This allows to assume that, in natural environments, this species could live in low oxygen and high temperature conditions. Like *H. latifasciata*, records of post-larval migrations from the ocean to freshwater could be considered as an indicator of an amphidromous life cycle for this species (Sánchez-Garcés, unpubl. data).

The species *A. transandeanus* has occurrences from 0-120 m high in Colombia, being very common in estuaries and small coastal ravines, as well as in the great rivers that flow into the ocean. Direct observations in the Valle river and clear water tributaries of the Anchicayá, Cajambre, Calima, Dagua and Yurumanguí rivers, have allowed to determine that this species has a preference for hydro-morphological units like run and pools, which are characterized by water at low speeds with moderate current and a substrate formed by fine sands near plant material deposits and in clay formations of the shores (Sánchez-Garcés pers. obs). Longitudinally, *A. transandeanus* is a species found several kilometres away from the coast, with Regan (1913) reporting it in the Condoto River (tributary of the river San Juan) at more than 150 km of distance from the coast. In Ecuador, in the province of Esmeraldas, it is associated with rocky bottoms, moderate in current and inhabiting the middle and upper parts of medium and large rivers of the Santiago-Cayapas system basin, where it is not very abundant, being present up to 400 m high (Jiménez-Prado *et al.*, 2015). In Costa Rica, Bussing (1998) reported that this species feeds on large amounts of detritus, chironomids, microbivalves and filamentous algae.

Regarding the genus *Sicydium*, distribution patterns for Mexico and Central America suggest that their presence is related to coastal mountain ranges, as well as to the width of the coastal plain, which can be explained by the amphidromous life cycle of the members of this genus (Lyons, 2005). For the Pacific Region at the Chocó Biogeographic

region, the northern rivers (Juradó, Jurubidá, Nuquí, Valle) have similar conditions to those of Central America, in that the presence of The Baudó highland leaves a narrow margin between the western Andean mountain range (Cordillera Occidental) and the coast, and the rivers in this area are short and steep and are suitable for *S. salvini*, a species widely distributed in Central America but recently recorded in the Valle River (Castellanos-Galindo *et al.*, 2011).

Towards the centre and the south, the rivers (Mira, Patía and San Juan rivers) present greater routes and discharges with a complex river system which, according to the hypothesis proposed by Lyons (2005) for Central America, should not have optimal conditions for the species of the genus *Sicydium* to thrive. In these conditions, larvae or juveniles may starve during migration between the ocean and the habitat suitable for adults if the distance is too long (approximately 60-75 km or more). However, this hypothesis is not consistent for the San Juan River basin, where a large number of *Sicydium* post-larvae annually migrate upstream looking for optimal conditions that are more than 100 km away from the coast. In addition, *Sicydium condotense* Regan, 1914 was described in this basin (which was not included in the present study, because it is only known by holotype) from an adult individual from the Condoto River (Tributary of San Juan) that is approximately 250 km from the coast. This means that there is a need to raise new studies on life cycle concerning the particular situation of the species associated with this type of large basins, even if it is known that some *Sicyopterus* species, the *Sicydium* sister genus, are found several hundreds of kilometres inland in Papua New Guinea (Keith *et al.*, 2011).

Other species of *Sicydium* with occurrences in the Pacific Region of the CBR are *S. hildebrandi* and *S. rosenbergii*, both endemic and without information about their biology and ecology. The first species has records up to 70 km from the coast in the town of Cisneros in the basin of the Dagua River at an altitude of 350 m. They are very common species in third and fourth order basins with a preference for rivers and streams of clear water in hydromorphological units like glides, runs, rapids, cascades and riffles. In northern Ecuador it is not abundant, it inhabits small streams with clear waters and moderate current and medium rivers such as Cachaví and Bogotá, and even large rivers such as Santiago in the city of Esmeraldas (Jimenez-Prado *et al.*, 2015). *Sicydium rosenbergii* was described from two individuals collected at 1067 m of altitude in the town of Paramba, northwestern Ecuador (Aguirre *et al.*, 2017). If the information is accurate, it would be one of the highest altitudes recorded for a species from the Sicydiinae group (McDowall, 2010).

The mountain mullet (*A. monticola*) is a species with large longitudinal and altitudinal displacements. It has been recorded in the basin of the Dagua River, at the town of Loboguerrero, 62 km from the coast and 660 m of altitude.



Figure 4. – Some amphidromous species from the rivers of the Chocó Biogeographic Region. **A:** *Eleotris picta*; **B:** *Gobiomorus maculatus*; **C:** *Awaous transandeanus*; **D:** *Hemieleotris latifasciata*; **E:** *Sicydium hildebrandi*.

Juveniles have a preference for creeks and third and fourth order rivers and inhabit hydromorphological units with moderate to rapid water velocities such as glide, run, rapid, cascade and riffle (Pulido and Sánchez-Garcés unpubl. data). Ribeiro and Villalobos (2010) observed in Costa Rica that this species has occurrences in sites with speeds ranging from high to moderate, resisting strong currents near waterfalls. In the Anchicayá basin it has been recorded feeding mainly on insects and crustaceans, presenting mature gonads in November, after determining that October is the month with highest abundance (Ospina and Restrepo, 1989). In the Dagua basin, two well-differentiated reproductive periods were recognized in April and September, which are associated with the rain peaks in April-May and October-November (Sánchez-Garcés *et al.*, 2011). In Ecuador, it lives in waters

with variable flow speed, going up to 650 m high, feeding on crustaceans, fish, insects and aquatic plants. Its reproduction is at different times of the year (Jiménez-Prado *et al.*, 2015) (Fig. 5).

Migration and fisheries

The high runoff caused by heavy rainfall generates large rivers with fast drainage, factors that negatively affect the fish's species richness in the region, mainly due to the increase in nutrient dilution, generating low productivity (Galvis, 1993). Also, the geological and biogeographic characteristics explain the lack of species with large sizes and the low abundance of the populations in the rivers that drain to the Pacific Ocean. The region is considered very poor with respect to inland fishery resources (Gutiérrez *et al.*, 2011).



Figure 5. – Representative habitat of freshwater amphidromous fishes in western of Colombia. **A:** photo of Valle River, 20 m collection site; **B:** Photo of Aguaclara River (Anchicayá Basin), 70 m collection site; **C:** Representative habitat in which post-larval *Awaous transandeanus*, *Hemieleotris latifasciata*, *Hemieleotris levis* and *Sicydium* spp. were collected in western Colombia. Photo of San Juan River, 18 m collection site; **D:** Type locality of *Sicydium hildebrandi*, photo of Dagua River in Cisneros, 350 m collection site.

Because of this situation, the amphidromous species that inhabit most of the water bodies gain some importance, and occupy different places of the basin with distances sometimes very far from the influence of the salinity and the sea.

In the Colombian Pacific Region, fish use is related to the zoning that exists along the basins, mainly due to the occupation of the territory by communities and fish supply, which decreases with altitude. This leads to variable practices and useful spaces depending on the proximity to the sea and the physiography of the basin.

Up to 100 m high, the use of fish is more diversified and increases with the proximity of the sea, as several secondary freshwater or marine-estuarine species are incorporated as a food source, some of them having commercial importance at a local scale. The amphidromous species of interest are for the inhabitants of the lower zones *A. transandeanus*, *E. picta* and *G. maculatus*, that are the ones that reach greater sizes.

The fishing methods vary according to the physiographic characteristics of the mid-high and low areas of the basins. Fishing is practiced following the biological cycles of the different species and some populations are dedicated to this activity in a specialized way. The marine-estuarine and amphidromous species decrease, increasing the supply of freshwater species that are harvested despite reaching small sizes. However, *A. monticola* due to its ability to climb the rivers up to 1500 m high (McMahan *et al.*, 2012) is impor-

tant in subsistence fishing and in small-scale trade in basins such as the Dagua River, where populations located at 800 m high, have fishing systems related to this species, taking advantage of migrations from the high areas of the rivers to their mouths to reproduce and then when adults go up to the river from May to June. To date, the purpose of this type of displacement is unknown (Sánchez-Garcés *et al.*, 2011). In Ecuador, *A. monticola* is recognized as a migratory species that descends to the sea to spawn and the juveniles return to the rivers until they mature into adults. Juveniles are not of great economic importance, and only large specimens are captured for subsistence. Some amphidromous species, mainly of the family Eleotridae, are important as food. In the Manabí province, the species *D. latifrons* is of great importance to rural and urban populations not only for fishing, but also as one of the most important species in aquaculture, especially in coastal areas. *Eleotris picta* is consumed locally and exported alive to the United States as well as *D. latifrons*, while *G. maculatus* is consumed in northern Esmeraldas, but is of little importance in the rest of the country (Jiménez-Prado *et al.*, 2015).

Besides fishing practices targeted towards adult stages of amphidromous species, there are other types of fishing activities that, despite being poorly documented, are part of the traditional fishing systems of Pacific communities. These systems usually take advantage of post-larval migrations

from the sea of different fish and crustacean species at certain times of the year and serve as an additional food source, which is also strongly linked in some regions to religious and cultural events (Sánchez-Garcés *et al.*, 2011).

In the Northern Pacific Region, in the Valle River, migrations where post-larvae of several species climb up the river from the ocean have been observed. The monthly migrations of *S. salvini*, *A. transandeanus*, *D. latifrons*, *Gobiesox juradoensis* Fowler, 1944, *Pseudophallus starksii* (Jordan & Culver, 1895) and *H. latifasciata* are accompanied by shrimp juveniles of the families Palemonidae and Atyidae, an event that is locally known as “viuda” and occurs generally during the highest tide of the month lasting between 2-3 days, which is the time that lapses between the arrival of the post-larvae to the beach and their entrance into the river. This event is important to the community which takes advantage of the massive post-larvae arrival to fish them on the beach, at the rivers mouths, with 99% of the catches corresponding to *S. salvini* (other species are discarded). In this period, catches can vary between 1.38 and 2.43 tonnes and is used as a food source by the same community or, as seen in recent years, to generated additional income from its commercialization at a local level (Castellanos-Galindo *et al.*, 2011; Sánchez-Garcés *et al.*, 2011; Blanco-Libreros *et al.*, 2015).

Towards the centre, the use of this migratory event has other spatiotemporal connotations and dynamics. Recent expeditions to the lower basin of the San Juan River, allowed to recognize that this only occurs during a certain time of the year, between the months of February and March, where two migrations can occur with a time difference of approximately two weeks, with variable composition, proportion and abundance of species.

The communities located in this area are mainly indigenous belonging to the Wounaan community, who share the territory with Afro-descendant communities and name this activity “chaupisa”, which converts to “chaupisa grande” when the composition is mainly of post-larvae of *Sicydium* sp., *A. transandeanus*, *Hemileotris* spp, juveniles of *G. maculatus* and larvae of palaemonid shrimp in similar proportions and the reference to “grande” (big) is due to the larger size of *Sicydium* post-larvae compared to the other species. On the other hand, the “chaupisa pequeña” (small chaupisa), is notable for being composed mostly of individuals of *H. levis* and shrimp, accompanied by the fish species mentioned above but in minimal proportions (< 10%).

The lower San Juan basin located between 0 and 100 m in altitude in the Buenaventura ecoregion, has an average annual precipitation of 6900 mm, an average temperature of 25.5°C and relative humidity between 90 and 100%. This basin combines alluvial and deltaic plains at its mouth, that are strongly influenced by the tidal regime, with low salinity and high turbidity in the coastal zone, due to the impact of the river discharge with an average flow of 2080 m³/s.

The delta of the San Juan river begins approximately 50 km from the sea, covering an area of 800 km² and a coastline of roughly 44 km in length, including the main channel of the river, five arms (Togoroma, Charambirá, Cacagual, Chavica and San Juan), estuaries and estuarine bays (Burgos, 2012). The characteristics mentioned above, as well as species composition and temporality, influence the fishing practices. These practices are done in the river and distributary channels, where the flow restricts fishing to the shoal in schedules without tide influence, but with a compulsory use of boats to look for post-larvae. As in the case of the “viuda”, “chaupisa” fishing is carried out using mosquito nets, although some inhabitants of the indigenous communities still have the tradition of catching them with baskets or containers made from vegetable fibres.

Information provided by inhabitants of the indigenous communities indicate that approximately 40 years ago the “chaupisa” arrived to the population of Noanamá, approximately 180 km away from the sea, but today, the exploitation takes place until the Population of Pangála that is approximately 100 km from the sea, with a decrease in the quantities captured, phenomenon attributed to the changes in the river conditions and to an increase in the population at the lower parts of the basin, generating a greater fishing pressure.

Fishery of amphidromous species in southern Colombia and northern Ecuador, as well as the rest of the eastern Pacific coast, has been poorly documented. Recently, Jiménez-Prado (2014) referred to the post-larval fishery of *Sicydium cf. rosenbergii* in the population of Esmeraldas on the northern coast of Ecuador, citing some works that mention this type of fishing for the coastal zone of Tumaco in southern Colombia and the rivers Santiago and Esmeraldas in Ecuador, where it is known as “chautiza”. The practice of this activity in this area, unlike what happens in the north and centre of Colombia, occurs between February and April, a period that coincides with the period of greatest precipitation, but at the same time with the end of the winter period. This is a family or community type activity, rather than a commercial one.

Conservation threats

The biogeographic Chocó is recognized as one of the regions with greatest biological and cultural diversity in the world, being one of the areas with less intervention, but with increasing pressures associated with forest extraction, mining, expansion of industrial forestry and agricultural plantations, illicit crops and development projects without environmental or social considerations (Maldonado-Ocampo *et al.*, 2012; Tognelli *et al.*, 2016). The quick process is mainly due to the loss of habitats by activities associated with deforestation (with a resultant increase in sediment and erosion), pollution by sewage and fuels, modification of river beds and habitats by mining, construction of civil works and

water demand for domestic, recreational and agricultural use (Saunders *et al.*, 2002; Suski and Cooke, 2007).

The main factors that are causing changes in the dynamics of aquatic ecosystems and directly or indirectly affecting the amphidromous species of the region, are described below.

Mining

An increase in global gold prices in recent years has led to a sharp rise in legal and illegal mining activities (Hammond *et al.*, 2013; Tognelli *et al.*, 2016), affecting several major basins in the Pacific coast. Impacts have not been scaled in most cases, but some studies on the basins of the Dagua, Guapi, Iscuandé, Micay, San Juan, Tapaje and Timbiquí rivers in Colombia, as well as the Santiago-Cayapas basin in Ecuador, recognize damages associated with an increase in turbidity, alteration of the water table, changes in the hydraulic and geomorphological characteristics represented by instability of the channel due to channel enlargement (widening/deepening), lateral erosion in terraces, channel narrowing by discharge of surplus material, as well as contamination by fuels used in drilling machines and vehicle maintenance (Sánchez-Arriaga and Cañón-Barriga, 2010; González-Perafán, 2013; Jiménez-Prado and Rebolledo-Monsalve, 2015).

Regarding the effects on fish, increased sedimentation could cover most of the structural elements of the river channel, reducing habitat diversity within rivers and streams, leading to a lower diversity of species, a lower proportion of young species and a high proportion of fish that feed on the surface (Mol and Outboter, 2004). This coincides with observations from the Dagua river basin, where the omnivorous or generalist species were more abundant in areas with mining intervention, taking advantage of the allochthonous material dragged by the current. The opposite was observed with amphidromous species, very common in similar and nearby basins without intervention, which presented very low abundances or were absent (Sánchez-Garcés, pers. obs.). This was also observed in *Sicyopterus sarasini* in New Caledonia where nickel mining is important (Lord and Keith, 2008).

Changes in vegetation coverage

Riparian forests have a direct relevance for fish taking into account the characteristics of the rivers from the Pacific watershed of the Chocó Biogeographic Region. These rivers are short in distance but large in discharge, with significant variations in their flow due to heavy rainfall, permanent nutrient transport and low mineral levels in water, which hinders primary production. Therefore, the base of the food chain for fish and other organisms associated with the aquatic ecosystem is provided by the rainforest (plant and animal material) (Ospina and Restrepo, 1989; Gutiérrez *et al.*,

2011). However, the region has been subject of extractive and productive activities for more than 70 years, where logging started in the 1940s, consolidating itself as one of the most important economic practices in the region (Leal and Restrepo, 2003). Later on, oil palm monocultures, which in the case of the department of Nariño in southern Colombia reconfigured the territory, and where coastal municipalities such as Tumaco in 2000 had almost half its area planted with oil palm plantations (28,000 ha). This activity replaced farm and forest areas, with subsequent pollution problems on rivers and water bodies due to agricultural and industrial waste released from crops (Arboleda-Montaña, 2008), situation that is shared with the north coast of Ecuador, where the progressive expansion of oil palm plantations affected local rivers and estuaries, causing a decline in fish and shrimp populations (Jiménez-Prado and Rebolledo-Monsalve, 2015).

Riparian vegetation greatly influences fish communities, with evidence of the importance of allochthonous material in some ecosystems, where the absence or reduction of this material can decrease the number of species, their densities and biomass, as well as growth, reproduction and survival rates (Casatti *et al.*, 2012). Many characteristics (biological, physical or chemical) of the different types of aquatic ecosystems depend on riparian vegetation and this influence is expressed on habitat diversity and structure (influence on the hydraulic profile, shelter and substrate supply for species), in water quality, flow regime or at the food chain level (Casatti, 2010). That is why ecological relationships in the Pacific rivers begin with the allochthonous material that falls into the water and serves as direct food source for some fish species, but is also transformed by mechanical processes or biological activity by benthic detritivorous macroinvertebrates and shrimp, which in turn, play an important role in the diet of amphidromous predatory species such as *A. monticola*, *A. transandeanus*, *E. picta*, *G. maculatus*, *Hemileotris* spp. in different developmental stages (Ospina and Restrepo, 1989; Sánchez-Garcés, pers. obs.).

Reservoirs and dams

One of the greatest pressures exerted on the populations of amphidromous species is the construction of dams, since they act as barriers for the migration and movements performed by these species (Walter *et al.*, 2012; Keith *et al.*, 2015). There are few studies that determine the impact of such barriers on migrations at the population or assemblage level, evaluating seasonal patterns (Rolls, 2011) and the effects of dams on tropical ecosystems is severely limited (Greathouse *et al.*, 2006). The impact of a dam on communities dominated by diadromous species depends on the height and distance from the sea to the dam (Joy and Death, 2001) and discharge of the dam.

In Puerto Rico, places without dams or areas under the barriers, have abundant and diverse native ichthyofauna and

shrimps, in contrast with predatory species (Mugilidae, Eleotridae and *Awaous* spp.) that are missing upstream from the dams. Likewise in Costa Rica, the loss of migratory species of fish and shrimp upstream could affect the community structure and biotic interactions, as well as the functional processes of ecosystems, such as the decomposition of organic matter, in which these species play an important role (Anderson *et al.*, 2006). Species of interest in recreational fishing and of value as food resource for local communities have also been lost, such as *Joturus pitchardi* Poey, 1860 (Mugilidae) (Anderson *et al.*, 2006). This situation is similar to what happened in the CBR at the Colombian Pacific Region, where three reservoirs have been built, two of them with special relevance: low and high Anchicayá dams. These dams are located at 215 m and 655 m, respectively, and have become barriers to the amphidromous fish species, which are not registered upstream of both dams, but downstream environments harbour species such as *A. monticola*, *A. transandeanus*, *D. latifrons*, *E. picta*, *G. maculatus*, *H. latifasciata*, *P. starksii* and *S. hildebrandi* (Angulo *et al.*, 2011; Arboleda, unpubl. data 2014; Sánchez-Garcés, pers. obs.).

Besides acting as a barrier to migratory species, dams can cause massive mortalities due to the uncontrolled discharge of sediments, like the one that occurred in the Anchicayá river basin in 2001, where more than 500,000 m³ of accumulated sludge were illegally discharged by the operating company, affecting the basin along 60 km and killing aquatic biota (Briceño *et al.*, 2013). To date, the aquatic biota has barely begun to recover and mass migrations of *S. hildebrandi* and *Macrobrachium* spp. ceased to occur with the frequency and intensity of the years prior to the event, according to anecdotal evidence from riparian communities.

Pollution and sedimentation

The coastal areas of the region display high pollution levels owing to several activities carried out mainly in the areas of influence of Buenaventura and Tumaco in Colombia, related to maritime and port activities that generate oily residues. These populated centres also have problems with untreated wastewaters that are discharged directly to the coast or carried by rivers, which also transport industrial, oily and agrochemical residues generated from mining and agricultural activities along the main basins (Gutiérrez *et al.*, 2011). On the other hand, basins in the central and southern Colombian Pacific Region have serious problems because of an increase in coca illicit crops requiring an indiscriminate use of chemicals that are later discharged into rivers. This, combined with constant oil spills in basins like Dagua and Mira, places the region's aquatic ecosystems, and the associated biota, in a vulnerable situation (Tognelli *et al.*, 2016; Sánchez-Garcés, pers. obs.).

Because part of the life cycle of amphidromous species is spent at sea and/or in estuary, they are sensitive to coast-

al disturbances, such as physicochemical changes within marine environments. These changes can disturb larval development, longevity and the ability to avoid predators, as well as the ability to locate freshwater sources. Pollutants such as heavy metals, chlorinated hydrocarbons and petrochemicals are toxic to marine larvae and can form barriers that prevent recruitment between populations of different streams (Walter *et al.*, 2012).

With respect to the sediment contribution in the Colombian Pacific Region, the nine main rivers contribute an average of 5047 m³/s of water containing sediments and other contaminants. Basins like the San Juan River have a great influence contributing 41% of the total flow, while Guapi, Iscuandé, Mira and Micay rivers contribute 53% (Gutiérrez *et al.*, 2011). The increase of the sediment load has been, in most cases, because of mining-associated activities and erosion processes caused by the deforestation happening in several Pacific basins. The heavy load of suspended sediments delivers an excessive concentration of fine material that damages the fish. For Sicydiinae gobies, it affects its physiology, reproduction and migration, especially in larval and post-larval stages (Keith *et al.*, 2015), which could lead to an interruption of the recruitment processes of amphidromous species in basins with greater sedimentation problems.

Climate change

Considering that freshwater species have specific distributions, changes in temperature or physicochemical conditions in water resulting from climate change could be drastic (Tognelli *et al.*, 2016), even more if we consider that the CBR is home to a considerable number of endemic species. These endemic species include some amphidromous species that move between freshwater and seawater for reproduction and recruitment, activities that are correlated with rainfall, flood patterns, changes in air temperature and rainfall associated with El Niño–Southern Oscillation (ENSO). These parameters could vary in frequency and intensity with climatic changes, affecting the populations of migratory species (Jiménez-Segura *et al.*, 2016).

Among the possible effects caused by climate change are rise in ocean temperatures and seawater acidification, which could have an influence on the recruitment of amphidromous fish larvae as well as on the connectivity patterns by increasing larval mortality and by shortening this stage. Ocean acidification can cause physiological and behavioural changes in fish and larvae (Walter *et al.*, 2012), while rising temperatures could affect sensitive groups such as Sicydiinae gobies (Keith *et al.*, 2015).

On the other hand, the reduction of maximum discharges due to global warming could lead to conflict situations between the supply needs of human coastal populations and the minimum connectivity and discharge requirements or regime of rivers and streams (Blanco-Libreros *et al.*,

2015). This could also impact the optimal conditions for the amphidromous species to fulfil the migratory cycle between the marine and freshwater environments, endangering the viability of populations (Keith, 2003).

However, for the case of the Tropical Andes, there are no studies on the effects of climate change on freshwater biodiversity, despite the fact that the basins on the Pacific watershed are considered as vulnerable to the conditions generated by these global changes (Anderson and Maldonado-Ocampo, 2011; Tognelli *et al.*, 2016). This situation is similar in terms of unawareness of the possible impacts of global warming on estuarine fishes in most areas of South America, where the effects of climate change alone can only be predicted in general terms (Blaber and Barletta, 2016).

Future perspectives

Most of the rivers of the Pacific region of the CBR are unexplored, presenting great gaps in the knowledge of their ichthyofauna, such as distribution, biology and ecology, especially of the amphidromous species, some of them having unclear taxonomic status to date (Blanco-Libreros *et al.*, 2015). Therefore, it is necessary to carry out studies that generate useful information to propose management and conservation strategies for these species, considering that they are sensitive to habitat degradation due to changes in land use (Bell, 1999) and climate change (Walter *et al.*, 2012) and are exploited at different stages of their life cycle (especially in recruitment), making them vulnerable to overfishing (Keith *et al.*, 2015).

In addition to the gaps in biological information related to migratory events, there is also an important aspect related to fishing activity. At present, there are no records on the number of people engaged in extraction, volumes, harvesting efforts, marketing, as well as their variability over time.

Although information on this “occasional” type of fishery is difficult to collect, it is crucial to establish its sustainability in the short and long terms to allow the establishment of control measures aimed at the management of the fisheries in the different catchment basins that perform this type of exploitation (Sánchez-Garcés *et al.*, 2011).

In that sense, some parts of the Pacific coast of the CBR are important as key areas for the conservation of fish biodiversity, where amphidromous species represent the connectivity between coastal zones and freshwater systems. The San Juan delta and the Jurubidá and Valle basins in Chocó, the Patía and Mira rivers in Tumaco, the Esmeraldas basin in Ecuador are positioned as of great importance because of migratory events involving several amphidromous species (some of them endemic) and because of the link between the sociocultural system and the natural values and attributes. These attributes represent the way in which aquatic ecosystems still maintain their ecological integrity (structure, dynamics, functioning and self-organization capacity) and

are able to generate a set of services that are part of cultural practices at different spatial and temporal scales.

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